# COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, XI

## THE XYLEM OF PERESKIOPSIS AND QUIABENTIA

## I. W. BAILEY 1

Ouiabentia may be differentiated anatomically from Pereskia (1) by the characteristic development in young stems of a highly differentiated crystalliferous hypodermis in these genera (Bailey, 1961b); (2) by the absence of diagnostic forms of sclereids in their secondary phloem (Bailey, 1961a); (3) by the sporadic occurrence in their stems and leaves of the curious short cells with broad annular or helical thickenings which have attracted so much discussion in the mammillarias and other excessively succulent forms of the Cactaceae (Bailey, 1960); and (4) except in comparisons with Pereskia conzattii Britt. & Rose, Pereskia autumnalis (Eichlam) Rose, and Pereskia nicoyana Web., by the characteristic pseudopalmate or palmate vasculature of their leaves (Bailey, 1960).

At present uncertainties regarding the status of the numerous described species of *Pereskiopsis* and *Quiabentia* are fully recognized by many taxonomists. Owing to these uncertainties and to the wide ranges of structural variability, not only in the same clone when grown under different environmental influences, but also in different parts of a single adult plant, it seems advisable in a preliminary investigation of the xylem to concern oneself largely with ranges of anatomical variability at a generic level rather than with possible structural differences between putative species and geographical races of the two genera.

The anatomical data presented in the following pages are based upon the investigation of 33 collections of *Pereskiopsis* from various parts of Mexico, kindly preserved for me largely by Norman Boke, R. L. Dressler, Efraim Hernández X., Myron Kimnach, and R. V. Moran. Twenty-nine of these collections exhibited more or less reliable affinities to the following putative species: *P. aquosa* (Web.) Britt. & Rose three collections, *P. blakeana* Ortega two, *P. chapistle* Britt. & Rose five, *P. diquetii* Britt. & Rose one, *P. gatesii* Baxter one, *P. pititache* Britt. & Rose three, *P. porteri* (Brand.) Britt. & Rose seven, *P. rotundifolia* (DC.) Britt. & Rose one, *P. scandens* Britt. & Rose one, *P. spathulata* (Otto) Britt. & Rose two, and *P. velutina* Rose three. There is no reliable clue at present to the affinities of four other collections.

In the case of Quiabentia, I have material of Q. aff. chacoensis Backbg.

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collected by Carenzo and Legname in the Jujuy Province of Argentina, of Q. pereziensis Backbg. collected by Cárdenas in Bolivia, and of Q. zehntneri (Britt. & Rose) Britt. & Rose obtained from a cultivated clone by Boke.

From the point of view of the phylogeny of the dicotyledons as a whole, the cambium and xylem of *Pereskiopsis* and *Quiabentia* have attained a high general level of evolutionary specialization comparable to that which has occurred in *Pereskia* and in a number of dicotyledonous families (Bailey & Srivastava, 1962). The fusiform initials of the cambium are comparatively short and tend to become arranged in stratified or "storied" patterns. The vessel members are short and have simple porous perforation plates; the wood parenchyma strands are short and of scanty paratracheal distribution in denser parts of the secondary xylem; the libriform fibers which may be septate or non-septate function in the storage of starch; and the rays are multiseriate, uniseriate ones having been phylogenetically eliminated. It should be noted in this connection, however, that in *Pereskiopsis*, as at times in *Pereskia*, the vessels which commonly are diffusely distributed either singly or in small clusters frequently exhibit aggregation into concentric zonal patterns in association with varying

proportions of wood parenchyma (Figs. 1-5).

It is in divergent trends of specialization (i.e., excessive broadening of multiseriate rays and the elimination of secondary walls and lignification within them) that stems of Pereskiopsis and Quiabentia differ most significantly from those of most species of Pereskia. In the case of arborescent forms of Pereskia, incipient evidence of the suppression of lignification, when present, is confined in P. sacharosa Griseb., P. grandifolia Haw., and P. bleo DC. to the innermost part of the first-formed multiseriate rays of roots (Bailey, 1963c). In arborescent forms of P. colombiana Britt. & Rose, P. guamacho Web., P. cubensis Britt. & Rose, and P. portulacifolia Haw., the phenomenon is accentuated in roots but not in stems (Bailey, 1963d). In the arborescent P. conzattii Britt. & Rose, P. autumnalis (Eichlam) Rose, and P. nicoyana Web., it occurs in a curiously modified form in the innermost parts of multiseriate rays in basal parts of large trunks (Bailey, 1963b). In contrast to these larger arborescent forms of pereskias, the smaller commonly more shrubby forms of P. humboldtii Britt. & Rose, P. weberiana K. Schum., and P. diaz-romeroana Cárd., with their not infrequent decumbent, scrambling or scandent branches, exhibit highly accentuated trends of divergent specialization in their roots, but only slight incipient evidence at times of the elimination of secondary walls and lignification in their stems (Bailey, 1963a). Within Pereskia, it is the highly scandent P. aculeata Mill. which differs most markedly from other species in having advanced trends of divergent specialization in both its roots and stems (Bailey, 1962).

In contrast to the arborescent species of *Pereskia*, the numerous putative species of *Pereskiopsis* are relatively low plants of shrubby form with stems or branches which frequently tend to be more or less decumbent, scrambling, or scandent. It should be noted that collectors find it difficult at present to locate plants of unmodified form in the wild. In many cases

specimens are obtainable only from plants cultivated in hedges or gardens, or, in remoter regions, from plants that have been cut back or variously mutilated by the activities of man. However, in all investigated collections, the ranges of variability in width, distribution, and internal structure of the multiseriate rays are extensive in stems from different parts of a single plant or clone. Furthermore, in the larger stems of all putative species of *Pereskiopsis*, there are conspicuous evidences of divergent trends of structural specialization, i.e., those leading toward more or less extensive elimination of secondary walls and lignification in rays and wood parenchyma.

In parts of some stems of *Pereskiopsis*, the first-formed secondary xylem resembles the wood of *Pereskia sacharosa* and of other arborescent pereskias. In such dense tissue (Fig. 1) comparatively narrow multiseriate rays, related to parenchymatous gaps of the eustele, are fully lignified, and relatively uniformly distributed as seen in transverse sections (Figs. 1 and 3). In subsequently formed secondary xylem (Figs. 3 and 4) the broadening rays exhibit more or less extensive patches of unlignified tissue which contain abundant druses of calcium oxalate. In addition, more or less extensive arcs or zones of unlignified wood parenchyma are of common occurrence (Figs. 4 and 5) not infrequently in association with zonal aggregations of vessels (Fig. 5).

In other stems of *Pereskiopsis*, having broader parenchymatous gaps in the eustele, the rays of the first-formed secondary xylem are broader (compare Figs. 3 and 9). The inner parts of such rays, related to interfascicular parts of the eustele, may be lignified, or unlignified (as in Fig. 9). Furthermore, in such rays the cells frequently are broader tangentially than radially. In subsequently formed secondary xylem, more or less extensive patches of unlignified ray tissue and unlignified zonal wood

parenchyma tend to occur (Fig. 7).

In transverse sections of some stems, aggregations of excessively broadened, lignified, unlignified, or partly unlignified rays may occur in wedges of secondary xylem which alternate around the circumference of a stem with intervening wedges of wood of denser, more normal structure, i.e., having narrower rays and a higher proportion of lignified vessels and libriform fibers. In these stems, the denser precociously flaring wedges of secondary xylem are related internally to the fascicular parts of the eustele. Such structural tendencies are diagrammatically illustrated in Fig. 2, a transverse section of a stem of *Pereskiopsis porteri*. In this stem, there are five conspicuous wedges of softer secondary xylem that are depressed below the outer boundary of denser, structurally more normal, intervening ones. The number of depressed wedges in the transverse section of the stem suggests a possible correlation with a 2/5 or 3/8 phyllotaxy.

That aggregations of broadened rays actually are related to phyllotaxy may be demonstrated by examining decorticated stems after treatment with phloroglucin-HCl (Text-fig. B), or by studying tangential longitudinal sections of the secondary xylem. As shown in the case of *Pereskiop-sis* aff. aquosa (Figs. 11 and 12), the connecting vascular tissues of the

leaf and areole are subtended in the secondary xylem by broad unlignified rays and relatively few tenuous strands of lignified libriform fibers and vessels. In passing downward from such a node through successively lower internodes to the next node of an orthostichy, the rays sooner or later become narrower and the strands of intervening lignified libriform fibers and vessels become correspondingly more numerous and broader. Thus, the structural differences between wedges of secondary xylem, visible in transverse sections of these stems, are due largely to the level at which the orthostichies are sectioned below their nodes.

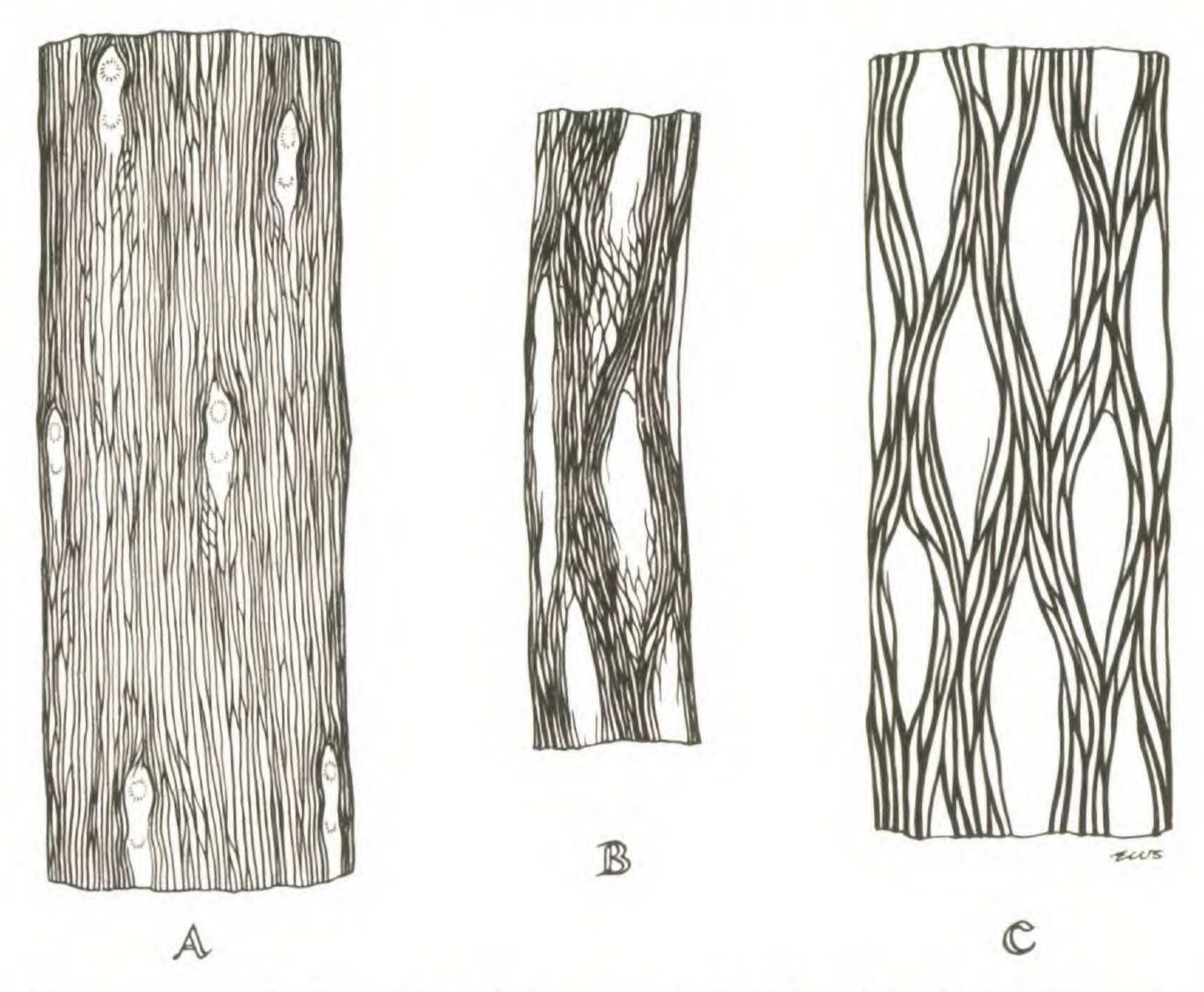
In some larger stems of *Pereskiopsis* aff. *aquosa* the aggregations of multiseriate rays subtending the node of an orthostichy, not only are very broad and unlignified as in Fig. 12, but also at times tend, just below the node, to fuse forming a broad wedge of unlignified tissue as seen in transverse sections (Fig. 13). In such wedges of unlignified parenchyma, narrow strands of lignified libriform fibers and vessels may be eliminated, their place being occupied by more or less vertically elongated, unlignified derivatives of the cambium between the broad fusing rays (Fig. 13).

It should be emphasized that in *Pereskia* the connecting vascular tissues of the leaves and areoles are jacketed in the secondary xylem by a very limited amount of unlignified parenchyma and are subtended by fully lignified tissue. When decorticated the stems resemble Text-fig. A, except that the rays are lignified throughout their radial extension outward in the secondary xylem.

In the case of *Pereskiopsis*, some stems exhibit comparable lignification in the earlier formed secondary xylem. In other stems or parts of stems, lignification tends to be suppressed in the secondary xylem for varying distances below the connecting vascular tissues of the leaves and areoles (Text-fig. B).

In basal parts of some of the largest stems of *Pereskiopsis* aff. *aquosa*, cells with broad annular thickenings occur, not only in elements of the primary body adjacent to vessels of the fascicular parts, but also in unlignified multiseriate rays of the secondary xylem. In the primary body, the cells are more or less elongated vertically and of fusiform outline (Fig. 16), and have more than one annular thickening per cell. In the rays of the secondary xylem, on the contrary, the cells are of rectangular form and contain a single broad annular thickening per cell (Figs. 15 and 17).

The xylem in roots of *Pereskiopsis* commonly exhibits divergent trends of anatomical specialization comparable to those that occur in roots of *Pereskia aculeata* (Bailey, 1962), *P. cubensis*, and *P. portulacifolia* (Bailey, 1963d). The inner parts of multiseriate rays related to protoxylem poles of the primary body tend to be unlignified. In the outward extension of these rays, and in those subsequently formed, there tend to be alternating patches of lignified and unlignified tissue. In addition, more or less extensive arcs or zones of unlignified wood parenchyma are of not infrequent occurrence. However, in general, the divergent tendency toward suppression of lignification tends to be more highly accentuated in stems than in roots of *Pereskiopsis*. This is in contrast to what happens in most species



Text-figs. A-C. Decorticated stems treated with phloroglucin-HCl, natural size. A, Quiabentia aff. chacoensis [Tucuman], B, Pereskiopsis porteri [Moran 7349], C, Quiabentia zehntneri [Boke].

of *Pereskia* where incipient trends of divergent specialization commonly are more advanced in roots than in stems.

In an earlier paper of this series (Bailey, 1961b), I noted briefly that where crystals of calcium oxalate are deposited in the fully lignified rays of arborescent pereskias, they occur as single large crystals or a few smaller independent ones, aggregations into typical druses being absent. Conversely, where multiseriate rays or parts of them are unlignified, druses of calcium oxalate are conspicuously developed. Since writing this paper additional collections of roots and stems of Pereskia and Pereskiopsis have been obtained. Although conspicuously numerous druses occur characteristically in unlignified ray tissue of these collections, minor aberrations may occur at times in rays that are composed of alternating patches of lignified and unlignified tissue. For example, in the case of Pereskia colombiana and P. guamacho, where single large crystals are unusually abundant in the lignified rays of stems, a few crystals of this form may occur in association with druses in unlignified patches of ray tissue in roots. Conversely, a few druses may occur at times in lignified parts of the rays in stems of Pereskiopsis. Most exceptional in this connection, however, is the occurrence of a few druses in the fully lignified rays of stems of the Peruvian and Bolivian pereskias.

According to descriptions and illustrations in the literature, Quiabentia

chacoensis, Q. pereziensis and Q. zehntneri are characterized by their erect stems bearing a number of upstanding coarse branches from which relatively short smaller ones diverge. All of the aerial parts of these plants (stems, branches, and leaves) are highly succulent. In my limited collections of the three species, the stems and larger branches have a greatly expanded pith and a relatively much reduced volume of secondary xylem. For example, in a stem of Q. pereziensis six centimeters in diameter, the pith has a breadth of three centimeters; in a stem of Q. aff. chacoensis, having a diameter of three and one half centimeters, the pith is two centimeters in diameter; and in a vigorous branch of Q. zehntneri, having a diameter of three centimeters, the pith is 18 millimeters in breadth.

It should be emphasized in this connection, however, that the accentuated succulence in stems and branches of *Quiabentia* is not due solely to excessive expansion of the soft tissues of the primary body with concomitant reduction in cambial activity. There is an obvious tendency in the secondary xylem, as in many stems of *Pereskiopsis*, toward increasing the proportion of unlignified tissue and concomitantly reducing the proportion of lignified libriform fibers and vessels. As indicated in Fig. 10, part of a transverse section of a vigorously growing branch of *Q. zehntneri*, the conspicuously broadened multiseriate rays are unlignified and contain numerous druses of calcium oxalate. This is true even in wedges of secondary xylem that are subtended by fascicular parts of the eustele and results in the formation of relatively widely spaced, exceedingly narrow wedges of lignified tissue composed of libriform fibers and vessels (compare Fig. 10 and Text-Fig. C.)

A similar tendency toward reduction of lignification occurs in stems of *Quiabentia pereziensis*. In Fig. 8, part of a transverse section cut near the base of a large stem, i.e., nearer the level of the ground, the narrower strands of secondary xylem are less diagrammatically distributed, being contorted by irregularities in the grain of the wood. Furthermore, they contain patches of unlignified wood parenchyma as well as lignified libriform fibers and vessels. The contortions of the grain and the excessive breadth of the unlignified rays in this stem are shown in tangential longitudinal section in Fig. 14.

The stems of *Quiabentia pereziensis* and *Q. zehntneri* in my limited collections, when decorticated and treated with phloroglucin-HCl, have conspicuous unlignified parenchymatous lacunae in the secondary xylem subtending the leaves and areoles at nodal levels (Text-fig. C), as in some stems of *Pereskiopsis* aff. aquosa and *P. porteri* (Text-fig. B). In the case of *Quiabentia* aff. chacoensis, the only stem of comparable diameter available to me at present has relatively long internodes and broad wedges of lignified xylem between its unlignified multiseriate rays, i.e., as seen in transverse sections of the stem. Furthermore, although there is some tendency for aggregation of broadened rays in the secondary xylem subtending the bases of the leaves and areoles at subnodal levels (Text-fig. A), these rays do not fuse to form large conspicuous unlignified parenchymatous lacunae comparable to those that occur in secondary xylem

of Q. pereziensis and Q. zehntneri. This suggests that the tendency toward increasing succulence of the wood in Quiabentia is less advanced in Q. aff. chacoensis than in the other two species of the genus. The suggestion is strengthened by the structure of one available root of Q. aff. chacoensis. As illustrated in Fig. 6, the xylem is of normal fully lignified structure and closely resembles that which occurs in the roots of Pereskia sacharosa (Bailey, 1962, Fig. 2) and other dicotyledons at equivalent levels of phylogenetic anatomical specialization. However, until extensive collections become available for studying the ranges of structural variability in different plants of the same clone or species, conclusions regarding anatomical differences between putative species of Quiabentia, as between those of Pereskiopsis, must remain largely tentative.

## SUMMARY AND GENERAL CONCLUSIONS

Evidence presented in this and preceding papers reveals incipient stages of divergent anatomical specialization in Pereskia, Pereskiopsis and Quiabentia. One of the most significant of these, for a clearer understanding of greatly accentuated succulence in stems of the Opuntieae and Cereeae, is the tendency toward increasing the circumference of the eustele with concomitant expansion of the pith during later ontogenetic stages of the development of the primary body. Incipient stages of this phenomenon are detectable in larger immature stems of various pereskias (Bailey, 1962, 1963c, 1963d). In such stems expansion of the parenchymatous interfascicular parts of the eustele and enlargement of the pith may occur after initiation of cambial activity in fascicular parts of the primary body. Enlargement of the pith is much accentuated in the basal parts of the large trunks of Pereskia conzattii, P. autumnalis, and P. nicoyana (Bailey, 1963b). In these pereskias, multiseriate rays related to unlignified parenchymatous gaps of the eustele remain unlignified and their cells have a capacity for tangential expansion, thus facilitating additional increase in the circumference of the eustele and enhanced enlargement of the pith. As indicated in this paper, similar phenomena are of commoner occurrence in stems of Pereskiopsis and Quiabentia (Figs. 7, 9, and 10).

However, as indicated earlier in this paper, enhanced succulence in stems of *Quiabentia* and *Pereskiopsis* is not due solely to increasing the proportion of soft tissue in the primary body, with concomitant reduction in the volume of secondary xylem. There is obvious evidence of divergent trends of specialization in the secondary xylem itself, leading to increasing succulence by suppression of secondary walls and lignification in multiseriate rays and wood parenchyma. Although this phenomenon is largely confined in *Pereskia* to roots and to stems of the scandent *P. aculeata*, it becomes more or less highly accentuated in stems of *Pereskiopsis* and *Quiabentia*. Furthermore, there is a tendency in some stems of the latter genera for aggregations of broad unlignified rays to subtend the connecting vascular tissues of leaves and areoles at nodal levels. This phenomenon is particularly significant in attaining a clearer understanding of the origin and

development of huge parenchymatous lacunae in the secondary xylem of various representatives of the Cereeae and Opuntieae. The breadth, longitudinal extension, and structural details of such subtending succulent strands of secondary xylem vary more or less markedly at times even in different stems of the same clone or plant. Many of the more conspicuous structural differences appear to be correlated at least in part with variations in the diameter of the primary body, in the number of fascicular strands in the eustele, in the width of parenchymatous gaps between them, with changes in phyllotactic patterns from 2/3 to 3/8 and possibly to 5/13, and with variations in vigor of growth involving conspicuous differences in internodal elongation.

There are additional trends of divergent anatomical specialization that merit attention. One of these is the tendency to form zones of wood parenchyma as seen in transverse sections of stems. Such zonal patterns of wood parenchyma commonly are associated with concentric aggregations of vessels and appear to be correlated with seasonal variations in cambial activity and in the maturation of cambial derivatives. Although zonal aggregations of vessels and *lignified* wood parenchyma occur in the laterformed secondary xylem of large stems of several arborescent pereskias, incipient stages of the *suppression* of lignification in wood parenchyma of stems is largely confined in *Pereskia* to the scandent *P. aculeata*. In contrast to this, the suppression of lignification in wood parenchyma is of common occurrence in stems of the shrubby representatives of *Pereskiopsis* and *Quiabentia*.

A trend of divergent specialization, which does not occur in any of my numerous collections of *Pereskia*, is the sporadic occurrence in leaves and stems of *Pereskiopsis* and *Quiabentia* of the curious short cells with broad annular or helical thickenings which are so abundantly developed in more succulent representatives of the Cactaceae. The occurrence, distribution, and structure of these cells in *Pereskiopsis* and *Quiabentia* merit additional detailed investigation, since the study of more comprehensive collections of adequate material may yield clues regarding the origin, function, and phylogenetic significance of such curious cells in the Cactaceae as a whole.

It should be emphasized in conclusion that in the leaf-bearing Cactaceae accentuations of divergent trends of anatomical specialization are more or less closely associated with changes in the stature and habits of growth of the plants in which they occur. In arborescent forms of *Pereskia* (i.e., those having a more typically woody dicotyledonous habit of growth) incipient stages of divergent specialization in the xylem are rarely detectable in *P. sacharosa*, *P. grandifolia*, and *P. bleo*; more or less conspicuous in roots of *P. colombiana*, *P. guamacho*, *P. cubensis*, and *P. portulacifolia*; and confined in *P. conzattii*, *P. autumnalis*, and *P. nicoyana* to the first-formed secondary xylem in the basal parts of large trunks of the trees. On the contrary, the phenomena are greatly accentuated in roots of the comparatively low, shrubby forms of Peruvian and Bolivian pereskias, and in both roots and stems of the scandent *P. aculeata*. In contrast to this, all stems in available collections of the shrubby representatives of *Pereskiopsis* and

Quiabentia, regardless of variations in their habit of growth and in different degrees of succulence, exhibit more or less accentuated divergent trends of specialization in their xylem. Thus, the various representatives of Pereskia, Pereskiopsis, and Quiabentia may be arranged in an ascending evolutionary series of increasing divergent specialization. In this ascending phylogenetic sequence, the arborescent forms of Pereskia occur at the lowest level and the highly succulent forms of Quiabentia at the apex. Furthermore, the evolutionary series at least suggests that among surviving representatives of the family Pereskia sacharosa, P. grandifolia, and P. bleo have most closely retained the vegetative habit of growth and internal structure of ancestral Cactaceae.

From a purely taxonomic point of view, the structure of the xylem provides additional diagnostic criteria for differentiating *Pereskia* from the genera *Pereskiopsis* and *Quiabentia*. However, it does not at present provide a convincing argument for separating *Rhodocactus* from *Pereskia* or *Pereskiopsis* from *Quiabentia*.

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## EXPLANATION OF PLATES

(The black spots in unlignified tissue of Figs. 2-4, and 9-13 are druses. Those in Fig. 14 are starch.)

#### PLATE I

Figs. 1 & 2. Transverse sections of stems, 1, Pereskiopsis aff. chapistle [Boke B-3], inner xylem of a vigorously growing shoot 25 millimeters in diameter with a pith six millimeters in diameter,  $\times$  14. 2, Pereskiopsis porteri [Moran 7349],

part of a stem 18 millimeters in diameter with a pith three millimeters in diameter, × 11.

#### PLATE II

Figs. 3 & 4. Transverse sections of stems,  $\times$  11. 3, *Pereskiopsis* aff. *chapistle* [Boke B-3], inner part of a stem seven centimeters in diameter with a pith four millimeters in diameter. 4, *The same*, part of outer secondary xylem.

#### PLATE III

Figs. 5 & 6. Transverse sections of secondary xylem, × 11. 5, Part of outer xylem from the same stem as Figs. 3 & 4. 6, Quiabentia aff. chacoensis, section of a root.

#### PLATE IV

Figs. 7 & 8. Transverse sections of xylem, × 11. 7, Pereskiopsis aff. aquosa [Dressler], section of basal part of stem six centimeters in diameter with a pith eight millimeters in diameter. 8, Quiabentia pereziensis [Cárdenas], large root.

#### PLATE V

Figs. 9 & 10. Transverse sections of stems,  $\times$  11. 9, *Pereskiopsis* aff. aquosa [Dressler], xylem from a stem four centimeters in diameter with a pith 12 millimeters in diameter. 10, Quiabentia zehntneri [Boke], part of xylem from a stem four centimeters in diameter with a pith 14 millimeters in diameter.

#### PLATE VI

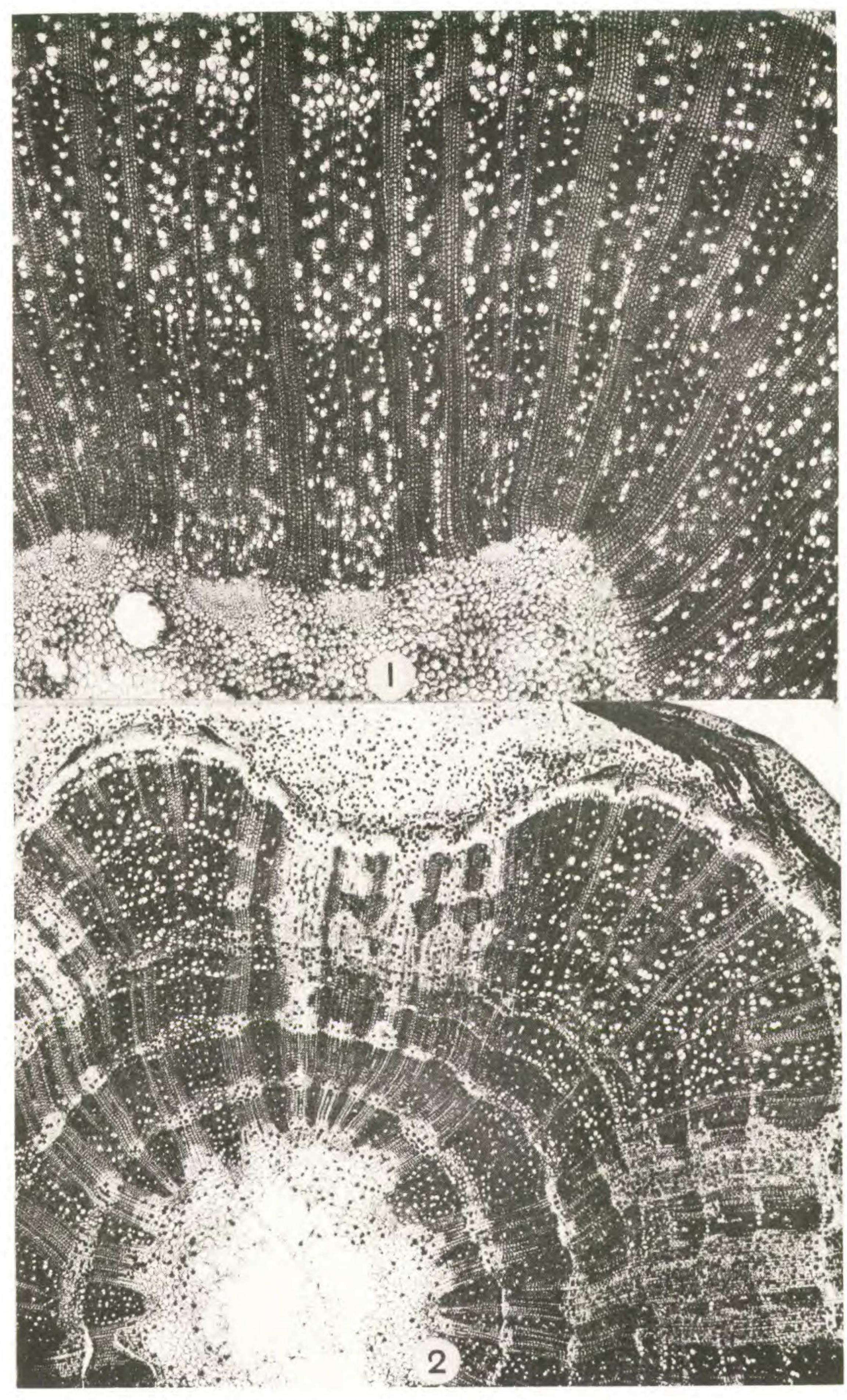
Figs. 11 & 12. Tangential longitudinal sections of stems of *Pereskiopsis* aff. aquosa [Boke B-31],  $\times$  7. 11, From a stem 23 millimeters in diameter with a pith seven millimeters in diameter, showing leaf traces and cylindrical vascular tissue of areole. 12, From a stem five centimeters in diameter with a pith nine millimeters in diameter.

#### PLATE VII

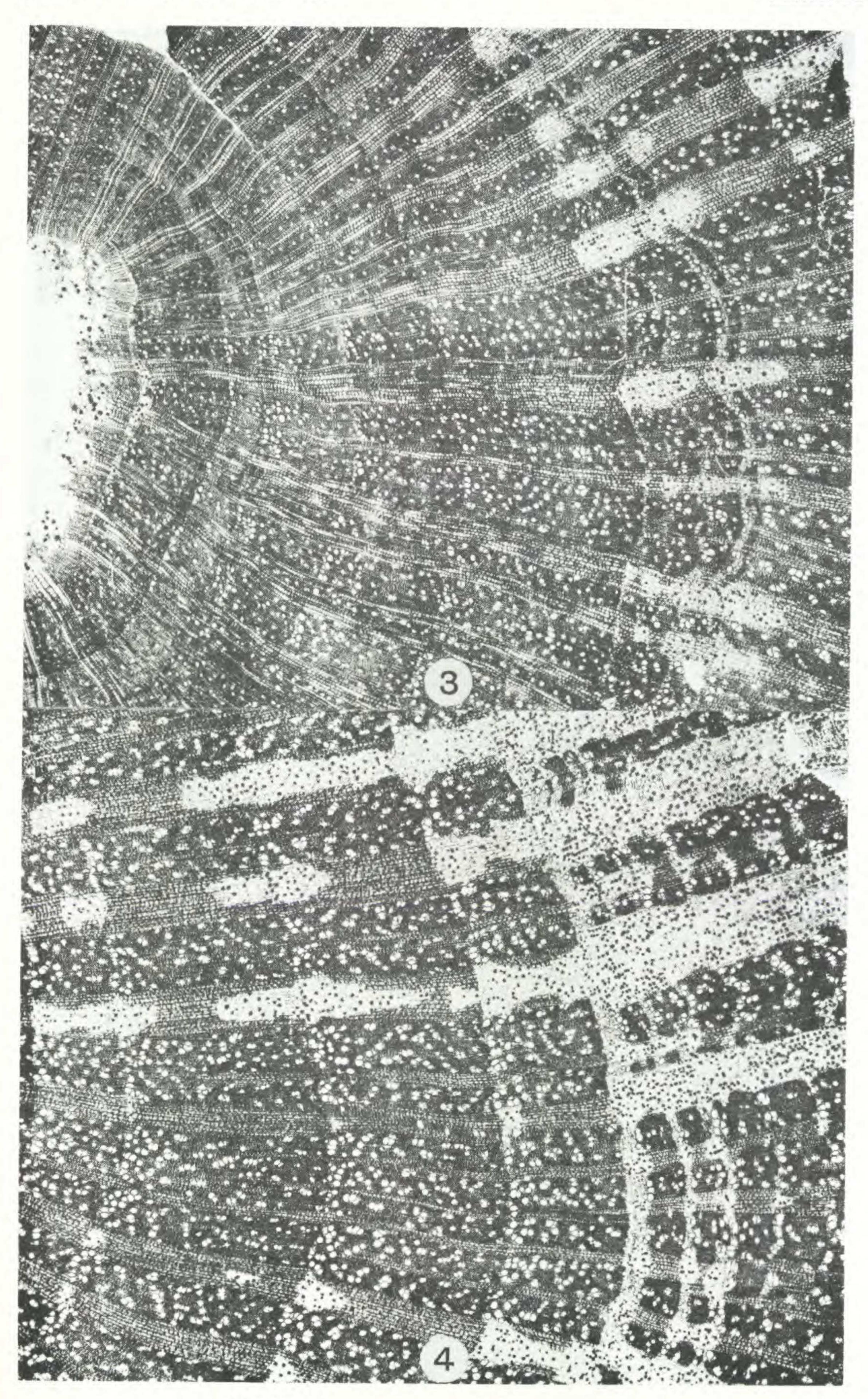
Figs. 13 & 14. Transverse and tangential longitudinal sections. 13, Pereskiopsis aff. aquosa [Boke B-31], transverse section of larger stem,  $\times$  7. 14, Quiabentia pereziensis [Cárdenas], tangential section of outer secondary xylem from a stem six centimeters in diameter with a pith 33 millimeters in diameter,  $\times$  43.

#### PLATE VIII

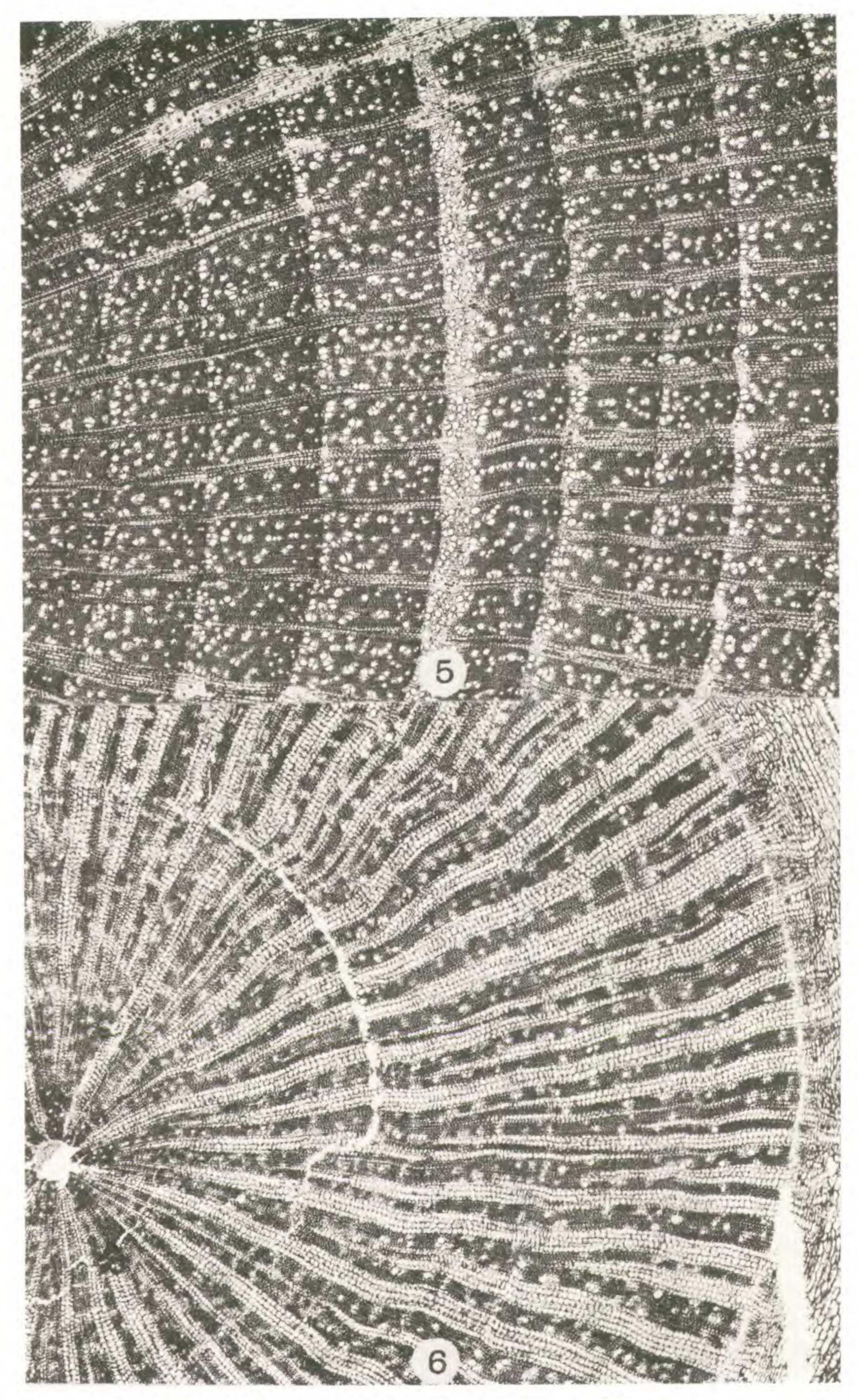
Figs. 15-17. Sections from the largest basal part of a stem of *Pereskiopsis* aff. aquosa [Dressler], × 88. 15, Transverse section of ray cells showing broad annular thickenings. 16, Longitudinal section of the outer part of the eustele showing fusiform cells with broad annular thickenings. 17, Radial section of a multiseriate ray showing single broad annular thickening in ray cells.



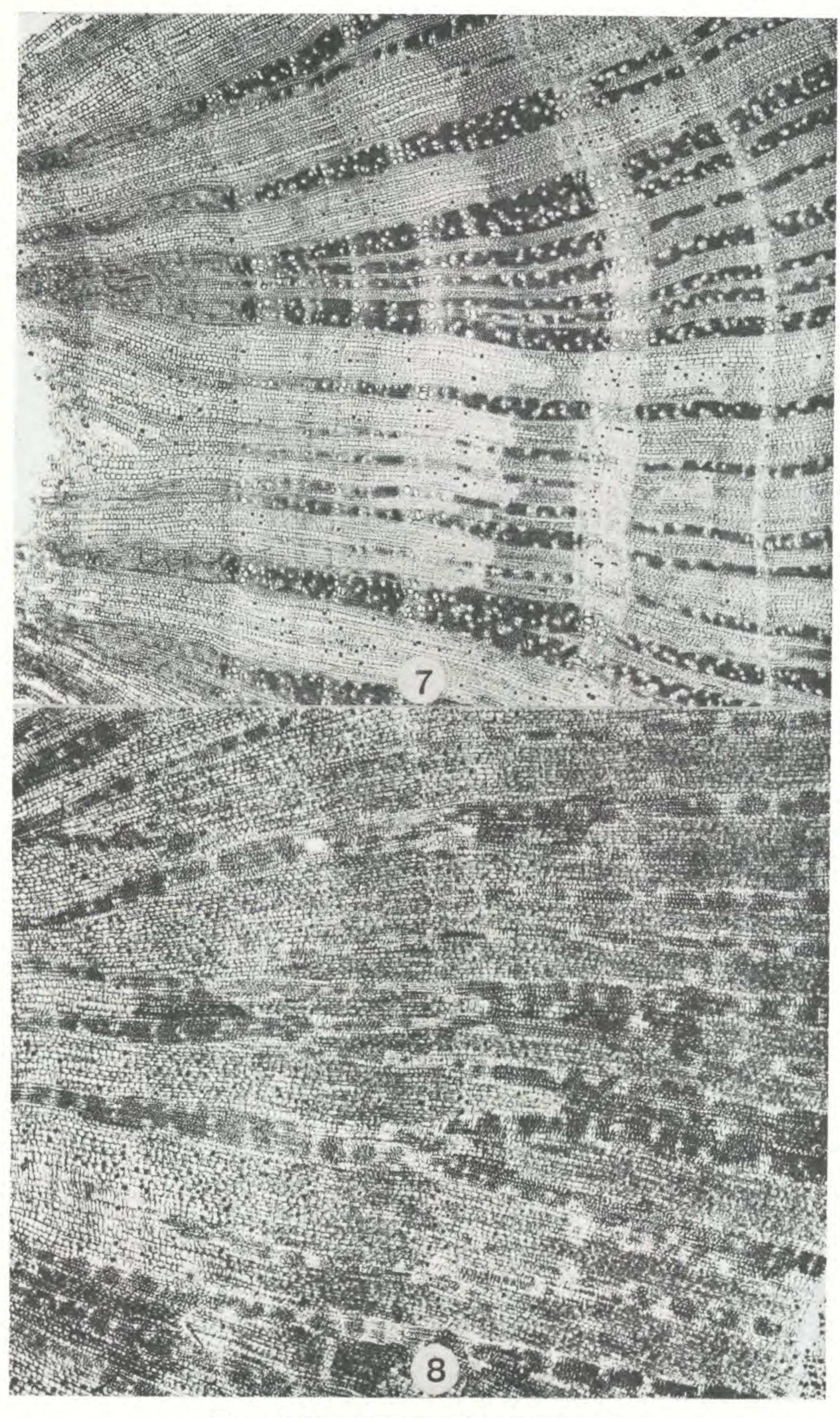
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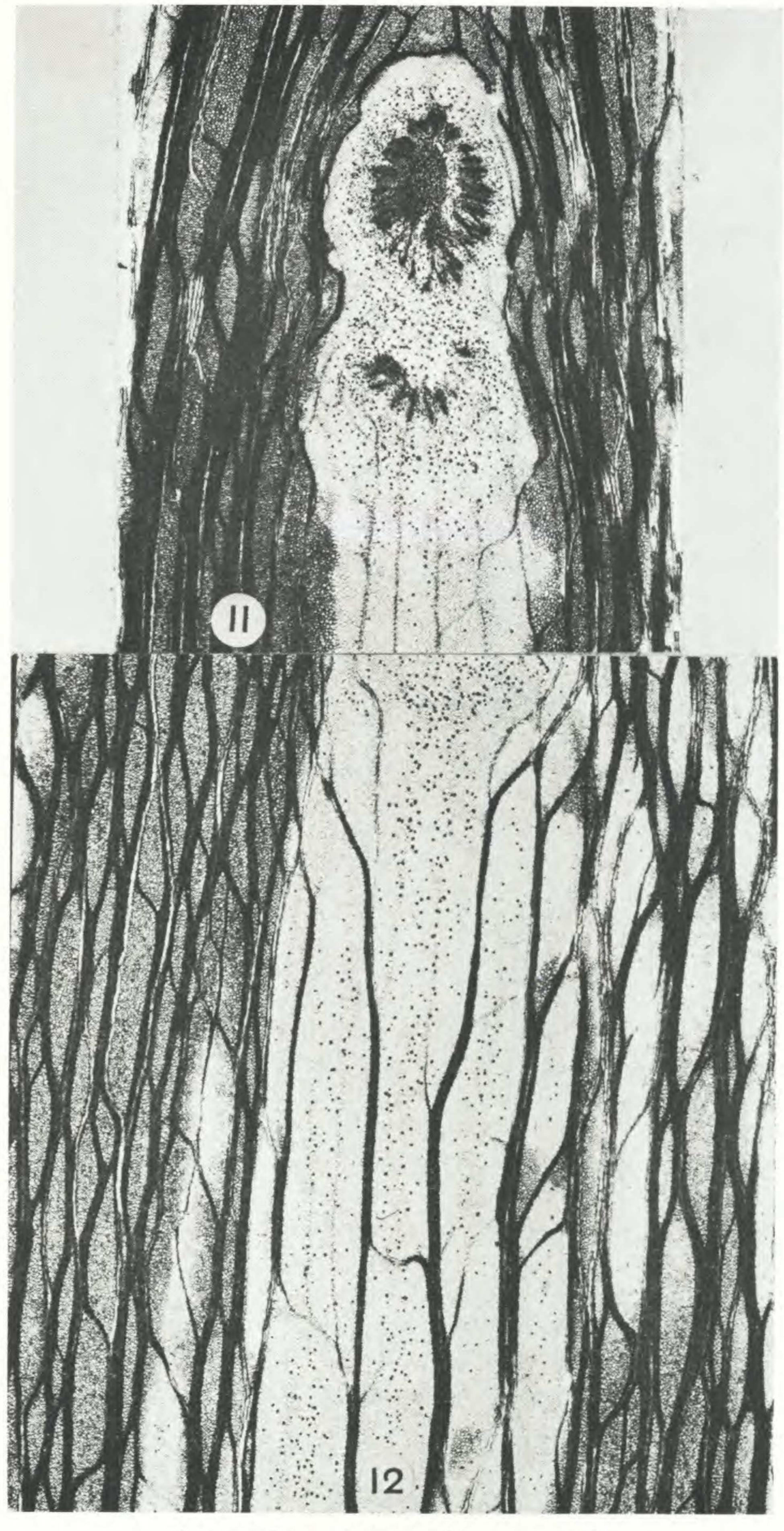
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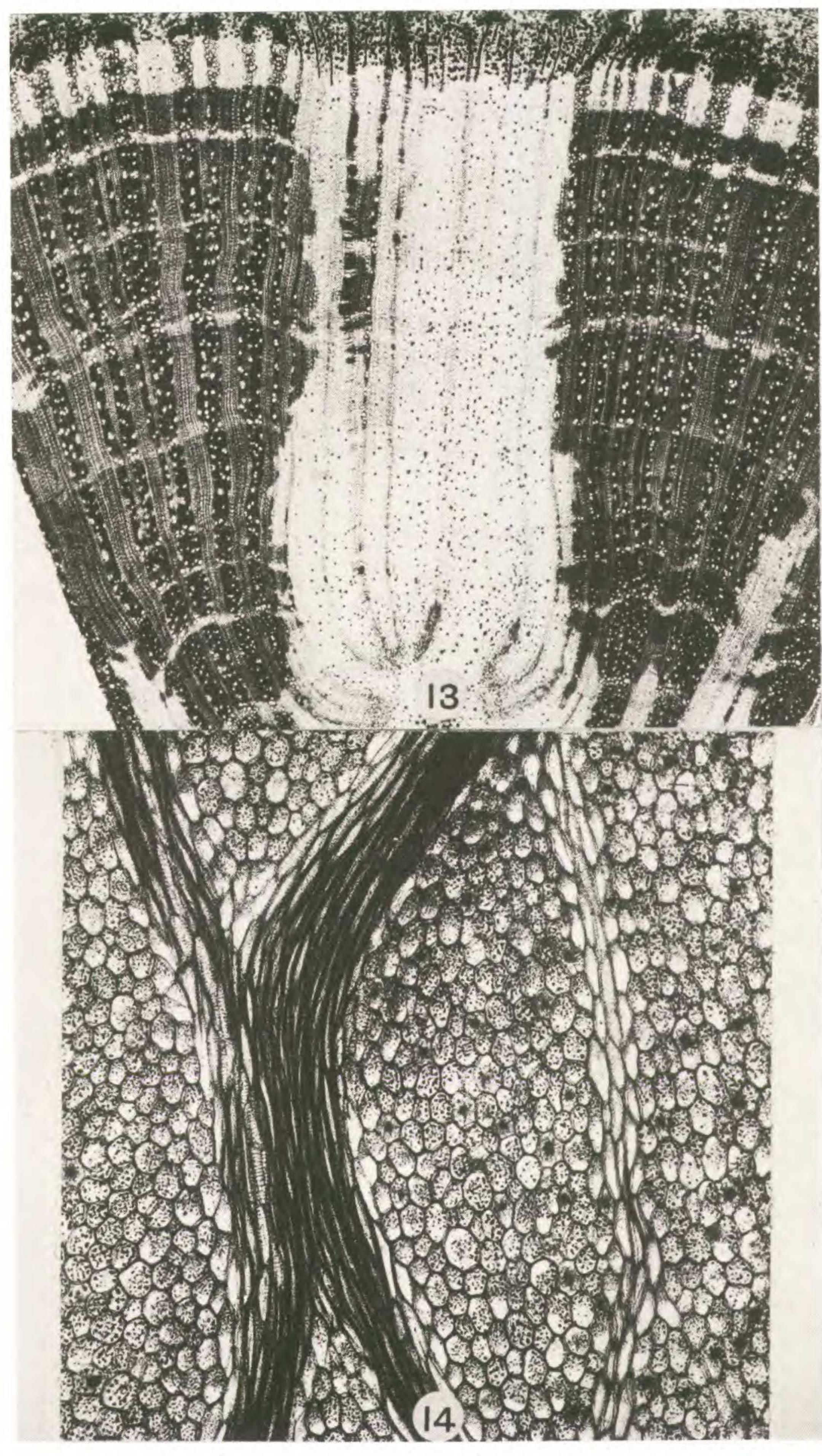
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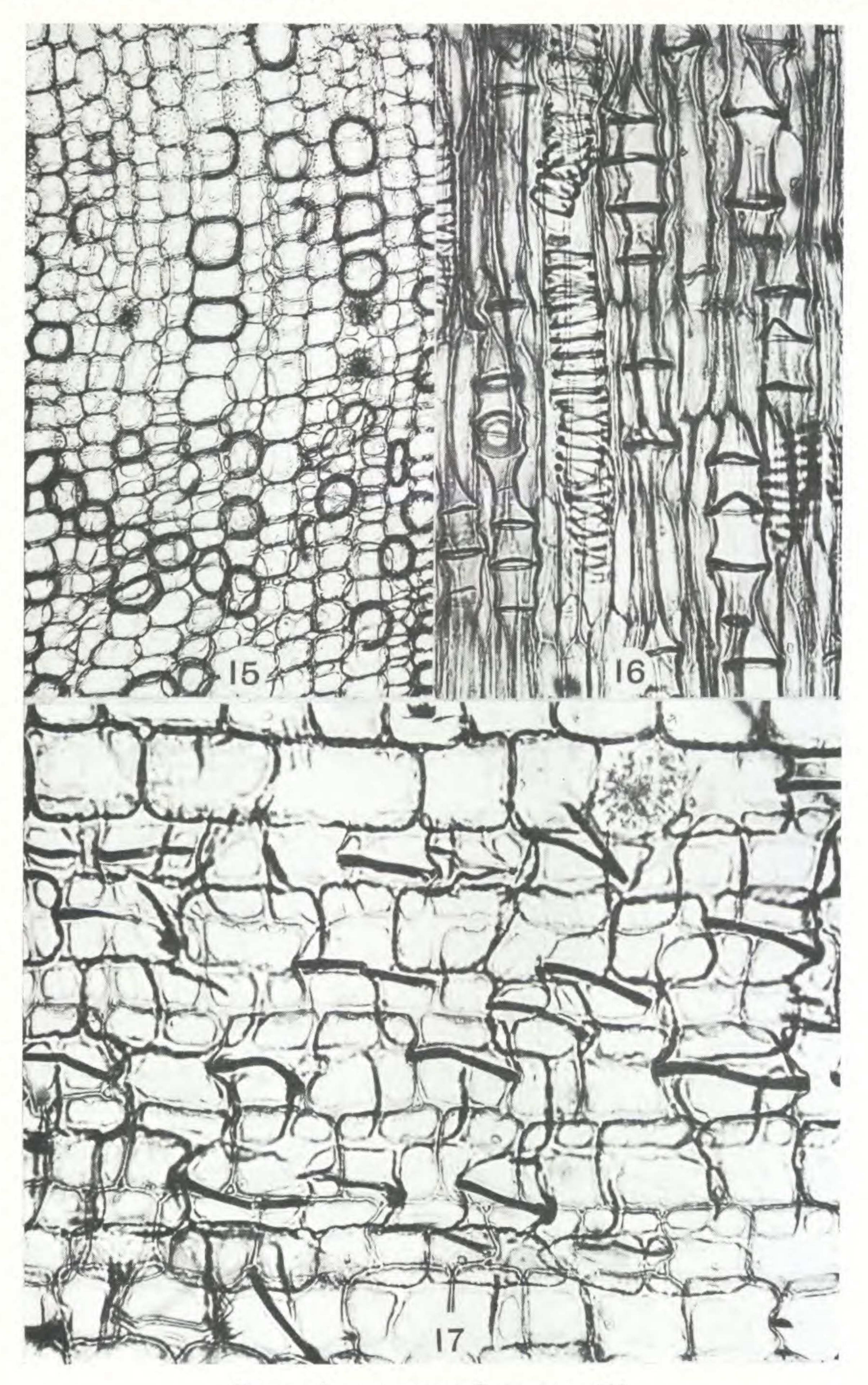
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Bailey, Leaf-bearing Cactaceae, XI